S.M. Gende · T.P. Quinn · M.F. Willson

Consumption choice by bears feeding on salmon

Abstract Consumption choice by brown (*Ursus arctos*) and black bears (*U. americanus*) feeding on salmon was recorded for over 20,000 bear-killed fish from 1994 to 1999 in Bristol Bay (sockeye salmon, *Oncorhynchus nerka*) and southeastern Alaska (pink, *O. gorbuscha* and chum salmon *O. keta*). These data revealed striking patterns of partial and selective consumption that varied with relative availability and attributes of the fish. As the availability of salmon decreased, bears consumed a larger proportion of each fish among both years and habitats. When availability was high (absolute number and density of salmon), bears consumed less biomass per captured fish, targeting energy-rich fish (those that had not spawned) or energy-rich body parts (eggs in females; brain in males). In contrast, individual fish were consumed to a much greater extent, regardless of sex or spawning status, in habitats or years of low salmon availability. The proportion of biomass consumed per fish was similar for males and females, when spawning status was statistically controlled, but bears targeted different body parts: the body flesh, brain and dorsal hump in males and the roe in females. Bears thus appeared to maximize energy intake by modifying the amount and body parts consumed, based on availability and attributes of spawning salmon.

Keywords Foraging behavior · Brown bears · *Ursus* · Salmon · *Oncorhynchus*

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Introduction

Foraging decisions by predators are a function of complex, and often dynamic, spectra of costs and benefits associated with energy gained and expended pursuing, acquiring, and handling prey (Stephens and Krebs 1986). Whether or not a prey item is attacked may reflect predator avoidance (Godin 1990; Sih et al. 1990), shelter or food preference (e.g., Duffy and Hay 1991; Francis and Conover 1994), or reproductive opportunities (Abrahams 1993). Once a prey item is acquired and subdued, however, the degree to which it is consumed may depend on attributes of the prey, such as energetic content, digestibility, and relative availability, and on attributes of the predator, such as physiological capability or degree of satiation (e.g., Greenstone 1979; Sih 1980; Penry 1993; Gill and Hart 1994). For example, a decrease in acquisition time can decrease amount eaten per prey, if organisms maximize the rate of energy intake by consuming the most profitable parts of the prey (e.g., Cook and Cockrell 1978; Sih 1980; Lucas 1985; Saether 1990).

Although consumption choice by predators has a strong theoretical background, field-based studies of consumption choice are often difficult because of large home-ranges or dietary breadth of predators, resulting in inaccurate sampling techniques and preventing precise quantification of all potentially important dietary constituents (e.g., Hutto 1990). Foraging by brown (*Ursus arctos*) and black (*U. americanus*) bears on spawning Pacific salmon (genus *Oncorhynchus*), however, provides an excellent opportunity to test predictions regarding consumption choice of a large, wide-ranging omnivore. First, salmon consumption has direct fitness consequences for bears. Populations of brown bears with access to salmon achieve heavier body weights, produce larger litters, and occur at higher population densities than those populations without access to salmon (Miller et al. 1997; Hilderbrand et al. 1999a). Second, diets of coastal bears are relatively simple in the late summer and early fall, consisting primarily of salmon (Hilderbrand et al. 1996). Although berries are also utilized in the late summer,

foraging efficiency limits intake rates when bears feed on berries (Welch et al. 1997), thus salmon provide the best opportunity to put on fat layers before hibernation. Third, availability of salmon to bears can be accurately recorded because salmon return to spawn in discrete geographic units such as streams or ponds, where they can be counted. Salmon abundance varies from year to year at a given site in response to variation in recruitment and fisheries and varies among sites with habitat quality (see Groot and Margolis 1991 for basic salmon life history information), providing a unique field experiment of consumption choice as it varies with availability. Finally, energetic "reward" for bears consuming salmon will vary with different attributes of the salmon, such as the sex and spawning status of the fish, and with the specific body part consumed. When salmon enter freshwater, feeding is arrested resulting in a fixed amount of energy to fuel migration and reproduction (Gilhousen 1980; Brett 1995). Salmon live for about 10 days in small systems (McPhee and Quinn 1998) before exhausting their energy reserves (Hendry and Berg 1999) and dying naturally (senescence). Thus unspawned fish (ripe) just entering the stream provide a much greater energetic "reward" than older fish, i.e., those that have been in the stream for many days and are approaching death.

The purpose of this study was to examine consumption choice of salmon by bears as it varies with relative availability and attributes of spawning salmon. We used foraging theory, coupled with knowledge of energy allocation in salmon, to predict consumption choices by bears. (1) As the availability of fish decreases, the proportion of biomass eaten per fish should increase. When availability is high, bears should selectively consume salmon and should maximize energy intake per fish by (2) consuming more biomass per ripe versus spawned-out fish and (3) targeting the roe in females. As male salmon do not have a localized lipid concentration such as roe, (4) the proportion of biomass consumed per fish should be higher in males as bears must consume more of each fish to obtain equal energetic rewards.

Materials and methods

General approach

We examined the carcasses of salmon found on foot surveys for evidence of consumption by bears from 1994 to 1999 at sites in southeastern and southwestern Alaska. The frequency of surveys and the nature of the data collected varied among streams and years. The sampling protocols were determined by access to the streams, the number of salmon carcasses, and by our evolving understanding of the patterns of consumption over the course of the study.

Study sites

Bristol Bay

Data were collected on two streams that feed into Lake Aleknagik in the Wood River Lake system of Bristol Bay. Hansen Creek is a shallow (10 cm deep), spring-fed stream approximately 4 m wide and 2 km long (Marriott 1964). During the spawning season (late July to mid-August), discharge varies little, even after rainfall. The water is clear and the stream channel has virtually no large woody debris or deep pools. Some cover is available to salmon in under-cut banks but the backs of salmon are exposed above the water in much of the stream, leaving them easily exposed to bear predation (Ruggerone et al. 2000). Bear Creek averages 5 m wide and 19 cm deep (Marriott 1964), and is more complex than Hansen Creek, with deep pools and woody debris. Spawning periods overlap but are slightly later in Bear Creek. The Pedro Pond system is a complex series of spring-fed ponds and creeks flowing into Pedro Bay of Lake Iliamna (Demory et al. 1964; Fig. 1.). We sampled four small ponds and four large ponds, all about 20–40 cm deep and five creeks connecting five of the ponds (10–20 cm deep, 2 m wide and averaging 64 m long (see Quinn and Kinnison 1999, Table 1). The water was very clear and depth did not change appreciably during the sampling period. Although the ranges of brown and black bears overlap in Bristol Bay, foraging on these creeks and ponds is almost exclusively by brown bears. No salmon other than sockeye were seen in Hansen Creek or the Pedro Pond system and sockeye constituted over 99% of the salmon in Bear Creek, with only an occasional chum salmon seen.

Southeastern Alaska

Seagull, Bear, and an unnamed creek, called Himmel for the purpose of this study, are all small, second- or third-order streams lo-

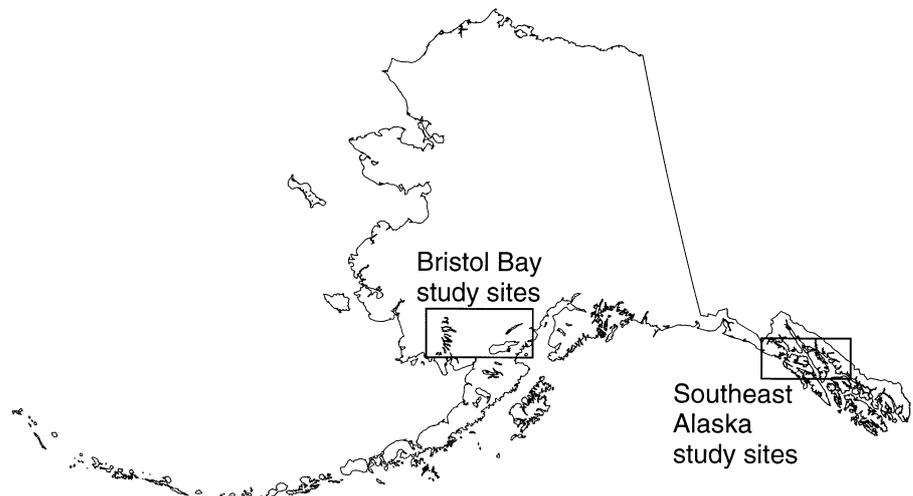**Fig. 1** General location of study sites in Alaska

Table 1 Average number of spawning salmon (run size) and salmon density (average run size/average area) for Hansen Creek (1997–1999) and a series of large ponds (*n*=4), small ponds (*n*=4) and small creeks (*n*=5) in the Pedro Pond system, Bristol Bay, Alaska between 1994 and 1999

Year	Hansen creek (area=8,000 m²)		Large ponds ($\bar{x}$ area =1180±234 m²)		Small ponds ($\bar{x}$ area =281±149 m²)		Small creeks ($\bar{x}$ area =109±90 m²)	
	Run size	Density	Average run size	Average density	Average run size	Average density	Average run size	Average density
1994			861.0	1.24	55.0	0.25	7.0	0.06
1995			878.0	1.13	117.0	0.54	39.2	0.36
1996			5.5	0.01	2.5	0.01	2.0	0.02
1997	8,845	1.11	9.5	0.01	0.5	0.00	0.0	0.00
1998	12,529	1.57	552.5	0.52	41.3	0.19	38.2	0.35
1999	20,000	2.50	526.3	0.51	7.4	0.34	3.7	0.03
Avg.	13,791	1.73	472.1	0.57	37.3	0.17	15.0	0.14

Table 2 Lower-jaw/body-length/body-weight relationships of pink, chum, and sockeye salmon used to estimate biomass of spawning salmon prior to consumption by bears

Species	Sex	Ripe			Spawned-out		
		Equation	n	R^2	Equation	*n*	R^2
Pink	Female	Weight =0.054e(0.0079×length)	102	0.77	Weight=0.0702e(0.0067×length)	68	0.59
		Weight=0.3386e(0.0202×lower jaw)		0.59	Weight=0.203e(0.0235×lower jaw)		0.58
	Male	Weight=0.054e(0.008×length)	251	0.85	Weight=0.0414e(0.0082×length)	22	0.88
		Weight=0.3202e(0.0155×lower jaw)		0.63	Weight=0.1861e(0.0188×lower jaw)		0.87
Chum	Female	Weight=0.1531e(0.0055×length)	133	0.56	Weight=0.0825e(0.0064×length)	91	0.83
		Weight=0.6855e(0.0155×lower jaw)		0.33	Weight=0.4793e(0.0171×lower jaw)		0.57
	Male	Weight=0.1479e(0.0058×length)	300	0.81	Weight=0.1469e(0.0057×length)	41	0.64
		Weight=0.4882e(0.0157×lower jaw)		0.71	Weight=0.4976e(0.0144×lower jaw)		0.66
Sockeye	Female	Weight=0.1186e(0.0062×length)	44	0.84	Weight=0.095e(0.0062×length)	31	0.83
	Male	Weight=0.0854e(0.0072×length)	84	0.87	Weight=0.0865e(0.007×length)	40	0.92

cated on the northeast corner of Chichagof Island and Margaret Creek is located on Revillagigedo Island. Each drains directly into the ocean over a large intertidal area that is submerged twice daily during high tides. Each stream is characterized by alternating riffles and pools, periodic gravel bars, and significant amounts of large woody debris. All of these streams vary in width between 2–7 m, depending upon location. Flows vary greatly with the duration and quantity of precipitation and depths fluctuate between 10 and 120 cm, so salmon are partially exposed during low flows and in shallow reaches.

Pink and chum salmon dominated the runs in southeastern Alaska (SEA). Chums generally entered the streams first (between 20 July and 1 August) and pinks entered shortly thereafter; runs normally lasted until mid-September. For much of August chums and pinks were present concurrently in the streams. Chichagof Island supports only brown bears whereas Revillagigedo Island has only black bears. Capture tactics were the same for both species and similar to bears in the Bristol Bay systems; bears captured salmon by pinning them with their paws or mouth and then carried them to the gravel bars or forest to be consumed.

Carcass surveys

Total run size was calculated for Hansen Creek in 1997–1999 and for the series of ponds and creeks in the Pedro Pond system 1994–1999 by counting the numbers of live, senescent dead, and bear-killed males and females. Hansen Creek was surveyed daily during the salmon run from 1997 to 1999 and habitats in the Pedro Pond system were surveyed just after the peak of the run (24–25 August) from 1994 to 1999 and on 2–5 other occasions earlier or later in most years. The Bear Creek in Bristol Bay was also surveyed in mid-August in 1997 and 1998. In SEA, streams were surveyed on 4–5 occasions, at about weekly intervals, from early July until early September annually from 1996 to 1999. Seagull, Bear, and Himmel Creeks were surveyed on four occasions (late July to early September) in 1997 and 1998, and Bear and Margaret Creeks were each surveyed once in 1996 (22 July) and 1997 (27 August) respectively. A tree stand was constructed on Bear Creek (SEA) for observing consumption choice by bears in 1998–1999. Deeper water and variable flows prohibited accurate counts of live fish (and thus run size) for streams in SEA.

Carcass measurement

When a carcass was found during a survey, the jaw length and body length (mid-eye to hypural plate) were measured (when possible) and the remaining biomass weighed. Body configuration, jaw shape, and gonad remnants were used to differentiate between species and sexes when a large fraction of the carcass was consumed. To estimate biomass consumed, we first estimated how much the fish weighed prior to consumption using either lower-jaw/biomass or body-length/biomass relationships established for at least 20 ripe and spawned-out fish of each sex and species (Table 2). Biomass consumed was then calculated by subtracting the biomass remaining from the estimate of its original biomass.

We also recorded the specific "body part" consumed by bears. Certain body parts of salmon seemed to be consistently consumed or avoided by bears irrespective of site, year, or salmon species

(see also Frame 1974). We recorded this phenomenon by separating parts consumed into five categories based on general body parts or relative amount of biomass consumed: body, belly, hump, brain, and skin. We considered the "body" consumed when a majority of the body flesh was eaten, occasionally leaving some flesh around the spine or skin. On average, 67% (range =44–99%) of the salmon biomass was consumed when the "body" was targeted. The belly was the area from the anus to just behind the pectoral fins and averaged 28% of the biomass of each fish (range =15–45%). The "hump" was the area posterior to the gill plate, anterior of the dorsal fin and above the lateral line ($\bar{x}$; range =2–7%). The "brain" was the cranial region above the eye and anterior of the operculum ($\bar{x}$; range =1–5%). Finally, the "skin" was designated when a bear clearly skinned the fish, leaving much of the body muscle remaining on the carcass, although some flesh was inevitably removed when bears targeted this body part ($\bar{x}$; range =1–3%). Due to the sheer numbers of bear-killed salmon in some of our streams, not all fish were weighed. For these fish we assigned the average biomass consumed when a similar combination of body parts was consumed in other fish where biomass was recorded. For example if a carcass was not weighed but the brain was consumed, we estimated that 2% of that fish was consumed. The relationships between body part eaten and amount of biomass consumed was established from measurement of over 8,000 carcasses over 6 years and thus we feel confident in assigning biomass consumed based on the body part targeted. In many cases more than one part was eaten (e.g., brain and belly) from a single fish and we counted these as separate instances of consumption for frequency analysis. In some ways this can be considered pseudoreplication (Hurlbert 1984) but we feel that each bite can be considered an independent decision by a bear. Furthermore, frequency comparisons were rerun on a subset of data where only one body part per carcass was used. For example, if a carcass had both the brain and belly consumed it was randomly assigned either brain or belly. The reanalysis resulted in identical results to the original comparisons and thus we present the comparisons where each body part was considered independently. To avoid repeated measurement, carcasses were either thrown into the forest or the bulb at the end of the lower jaw was cut off.

Availability and salmon attributes

Availability of salmon to bears seems to be a product of the volume of water in the pond/creek and density of spawning fish (Reinhart and Mattson 1990; Quinn and Kinnison 1999). Salmon availability could be accurately estimated at Hansen Creek and the Pedro Pond system because the geomorphology did not change within the sites (e.g., no deep pools, large wood, etc.), water depths remained constant during the spawning run, and total run size could be estimated. These sites support dramatically different numbers and density of spawning fish which vary annually within sites and within years among habitats, allowing us to document consumption under varying levels of availability (Table 1).

At all sites, attributes of each fish (species, sex, size, spawning status) were recorded only when they could be ascertained with a high degree of certainty. During foot surveys, the presence of eggs in the belly or near the carcass was used as an indicator of spawning status for females. However, it was much more difficult to assign spawning status for male salmon as they often die with some sperm remaining in their testes (Brett 1995). By observing foraging behavior of bears from tree stands and inspecting carcasses and testis size just after consumption, we were able to assign relative spawning status for a subset (about 20% of total observations) of male salmon at the SEA streams. We used all sites, when possible, to consider consumption choice as it varied with salmon attributes.

We considered all salmon with bite marks to have been killed by bears. We know that some dead salmon are scavenged (Quinn and Buck 2000) but, for the purposes of this study (i.e., examination of consumption patterns), we did not try to distinguish salmon killed from those scavenged. Consumption of salmon biomass by

other scavengers (e.g., eagles, gulls, mink) was extremely low compared to the degree of consumption by bears and we carefully examined all carcasses and counted only those that were clearly eaten by bears.

All comparisons of percent consumed were first arc-sin transformed (but presented as straight percentages). Multiple Chi-square tests were Bonferonni-corrected according to the number of tests performed. Statistical significance was considered at $\alpha=0.05$.

Results

Availability

A total of 20,230 bear-killed salmon were inspected from August 1994 until September 1999. In the Pedro Pond system and at Hansen Creek, the number and density of spawning salmon varied greatly among years and among habitats within years (Table 1) and bears responded to these differences by modifying the amount of biomass consumed per captured fish. Pooling all years, the average percent of biomass consumed per salmon increased as the average density of spawners decreased among habitats (ANOVA, $F =1930$, $P<0.001$; Fig. 2). At the small ponds and creeks of the Pedro Pond system, where salmon densities were generally low, bears consumed about 12% more of each fish than at the large ponds and about 37% more of each fish on average than at Hansen Creek where salmon densities were the highest.

We then analyzed the data more closely, using each site and year as a data point. In the large ponds and Hansen creek, where absolute abundance was high, the average amount of biomass consumed per fish decreased as the density of spawning salmon increased (Fig. 3a), reaching a threshold at Hansen Creek where only 25% of the biomass was consumed on average. However, at the large ponds in 1996 and 1997, the absolute number and density of spawning salmon was very low and bears consumed, on average, 66% and 83% of each killed fish,
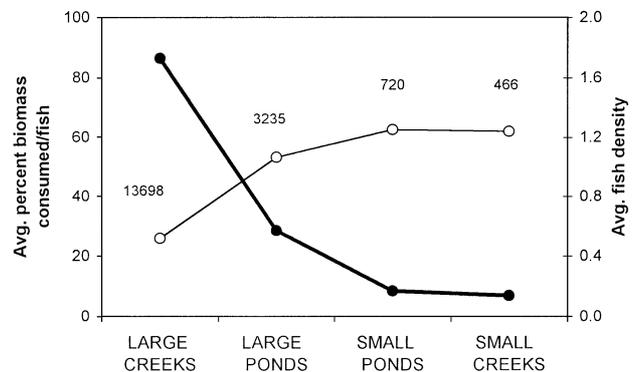
Fig. 2 Average percent of biomass consumed per captured salmon (○) relative to average density of spawning salmon (●) at Hansen Creek, and habitats of the Pedro Pond system, 1994–1999, Bristol Bay, southwestern Alaska. Sample sizes are located above open circles
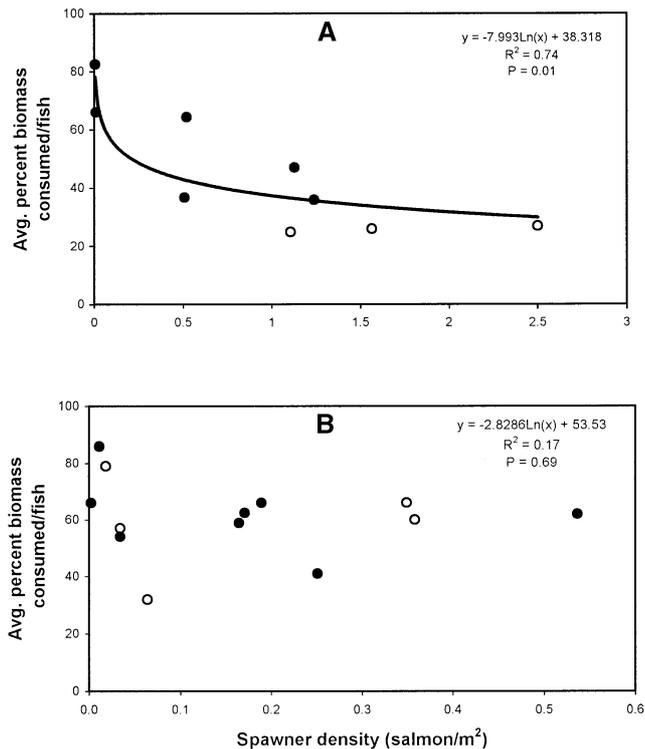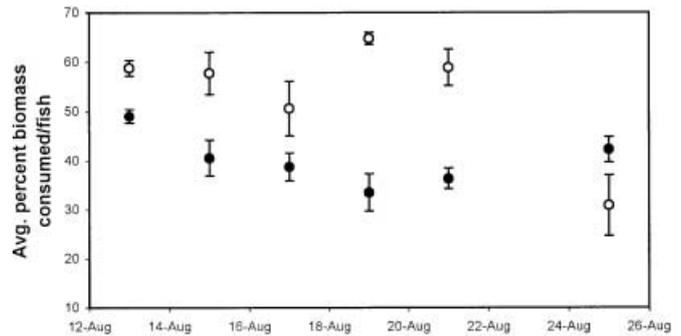
Fig. 4 Average percent biomass consumed per salmon by bears over the course of the spawning run in 1999 at the large ponds (●) and small ponds and small creeks (○) of the Pedro Pond system. Amount consumed per fish was significantly different during each survey date (*t*-test, $P<0.05$)

Table 3 Two-way ANOVA testing the effect of sex and spawning status on average percent of biomass consumed per fish for bears feeding on pink and chum salmon, 1998–1999

Source	Chums			Pinks		
	df	F	P	df	F	P
Sex	1	3.07	0.081	1	0.38	0.536
Status	1	199.94	0.001	1	120.06	0.001
Sex×Status	1	0.34	0.562	1	0.43	0.513
Error	447			290		

Fig. 3a,b Average percent biomass consumed per salmon by bears in relation to density of spawning salmon. **a** High salmon availability includes all large ponds in the Pedro Pond system (●) and Hansen Creek (○). **b** Small ponds (●) and small creeks (○) of the Pedro Pond system. Each data point represents a year (*n*=6 years, 1994–1999, for all small ponds and creeks except 1996 when no salmon spawned in the small creeks; Hansen Creek was surveyed 1997–1999). Note the different scales in spawner density (*x*-axis)

similar to proportions consumed at the small ponds and creeks. In these years it was difficult to find carcasses with anything more than the jaws and scraps of viscera remaining, as was often the case in the small ponds and creeks in all years. Consequently we found no relationship between the density of spawning fish and degree of consumption in these low-density habitats (Fig. 3b).

We also found differences in the degree of consumption within years among habitats. In 1999 the average amount of biomass consumed per fish was significantly higher on all six survey dates at the small ponds and creeks where the absolute number and density of spawning salmon was lower (Fig. 4). On average bears consumed 19% more of each carcass at the small ponds and creeks on each survey date. Thus, bears responded to changes in availability by altering the amount of biomass consumed per fish within habitats across years and within a year among habitats.

Salmon attributes

Spawning status could be ascertained for male salmon only when bears were observed catching and consuming

the fish from tree stands in SEA. Thus we could only compare the degree of consumption as it varied with both sex and spawning status for a subset of the data from SEA. For both pink and chum salmon, spawning status, but not sex, strongly influenced the degree to which a fish was consumed (Table 3). Pooling years, ripe fish were consumed to a much greater degree than spawned-out fish for both sexes of chum salmon (ripe females $\bar{x}\pm2.0$, *n*=209, spawned-out females $\bar{x}\pm1.8$, *n*=99; ripe males $\bar{x}\pm4.0$, *n*=100, spawned-out males $\bar{x}\pm3.7$, *n*=43) and pink salmon (ripe females $\bar{x}\pm2.2$, *n*=131, spawned-out females $\bar{x}\pm2.2$, *n*=60; ripe males $\bar{x}\pm3.7$, *n*=85, spawned-out males $\bar{x}\pm5.9$, *n*=18). Within years, ripe fish were consumed to a much greater extent than spawned-out fish for all species and sexes (Table 4).

Although a similar proportion of the biomass was consumed in both males and females, the body parts targeted by bears were sex-specific and remarkably consistent among sites, years, and species of fish. For all bear-killed salmon the belly was consumed much more often in females whereas the body, hump and brain were consumed more frequently in males (Table 5). Of the subset of fish killed in which spawning status could be determined, the belly was consistently consumed more often in ripe than spawned-out females for all species (Table 6). Similarly, the body flesh was consumed more often in ripe than spawned-out fish for male chums and female and male pinks.

Table 4 Average percent of biomass consumed per fish by bears feeding on ripe and spawned-out pink, chum, and sockeye salmon in Bristol Bay and SEA between 1997 and 1999

Year	Species	Sex	Avg. percent biomass consumed ($\bar{x} \pm SE$)				t	P
			Ripe	n	Spawned-out	n		
1997	Sockeye	Females	11.8±0.87	139	4.0±0.98	142	5.96	<0.01
1998	Chum	Males	49.8±5.34	24	1.7±2.58	6	8.83	<0.01
		Females	39.8±3.47	72	5.6±1.48	18	9.08	<0.01
	Pink	Males	57.7±4.7	52	9.5±5.48	4	2.81	0.01
		Females	54.6±3.43	54	5.1±1.36	18	13.4	<0.01
	Sockeye	Females	31.3±1.84	163	4.3±0.49	195	14.2	<0.01
1999	Chum	Males	51.1±4.4	76	8.2±4.28	37	6.99	<0.01
		Females	46.0±2.04	137	3.4±2.21	81	13.5	<0.01
	Pink	Males	41.8±5.67	33	4.6±7.57	14	3.72	<0.01
		Females	49.2±2.52	77	13.1±3.05	42	8.82	<0.01
	Sockeye	Females	25.6±2.26	109	7.2±2.18	26	5.87	<0.01

In addition to the clear relationship between consumption of body parts and the sex of the salmon, there was also evidence of size effects. This was most evident for sockeye salmon, for which we had the largest data set. We examined these data by comparing average body lengths of individuals when a part was eaten or not, as well as among size categories of fish (what percent of fish in a size class had a particular body part consumed; size classes arbitrarily chosen as 350–400, 401–450, 451–500, 501–550 mm). The salmon whose body flesh was eaten were significantly larger then those whose body flesh were not consumed for both females (body consumed $\bar{x}$ length =437±0.77 mm, n=1,182; body not consumed $\bar{x}$ length =431±0.54, n=3,083; t=5.44, P<0.001) and males (body consumed $\bar{x}$ length =454±1.22, n=1,036; body not consumed $\bar{x}$ length =441±0.79, n=2,045; t=8.24, P<0.001). The result is more apparent, however, if we compare the frequency of body consumed in the smallest versus largest size classes. Only 12% of female salmon in the smallest size class (350–400 mm) had their body consumed versus 29% in the largest size class (501–550 mm), and 29% versus 45% of the males (Table 7). Likewise, the brain was consumed more often in larger females (brain consumed $\bar{x}$ length =446±2.05, n=232; brain not consumed $\bar{x}$ length =432±0.46, n=4,033; t=6.89, P<0.001) and males (brain consumed $\bar{x}$ length =453±1.52, n=628; brain not consumed $\bar{x}$ length =444±0.75, n=2,453; t=5.24, P<0.001). The brain was eaten in only 3% of the females in the smallest size class compared to 15% in the largest class. The results were similar for males (15% vs 29%). Furthermore, the belly region was consumed more often in larger females (belly consumed $\bar{x}$ length =436±0.73, n=1,828; belly not consumed $\bar{x}$ length =430±0.55, n=2,437; t=6.76, P<0.001; 40% vs 54%). However, male salmon whose belly region was consumed were significantly smaller than those whose belly was not consumed (belly consumed $\bar{x}$ length =437±3.9, n=124; belly not consumed $\bar{x}$ length =446±0.68, n=2,957; t=–2.64,

P<0.008) with 8% of males in the smallest size class having their belly consumed versus 3% in the largest. No effects of body size were evident when the hump or skin was consumed for either sex.

Discussion

Consumption choice by animals is often difficult to study in the field because of the interconnected factors, such as reproductive opportunity or predator avoidance, that simultaneously influence a forager, as well as the obstacles associated with accurate quantification of food availability. Salmon consumption by bears provides an excellent opportunity to study consumption choice of a large, wide-ranging omnivore because of their relatively simple diet in the late summer, ease in determining salmon availability, and potentially important fitness consequences of consumption choice. Collectively, our results indicated that bears altered the biomass consumed per captured fish based upon the availability of salmon and elevated energy intake by consuming body parts highest in energy, depending on the sex and spawning status of each fish.

Availability

At the Pedro Pond system and Hansen Creek, bears consumed more biomass per captured salmon when availability was low versus high, both within habitats among years and among habitats within years. When salmon are abundant we infer that it is more energetically viable for bears to consume only the high-energy body parts from a carcass, drop it, and acquire another rather than continuing to consume the carcass "in hand". These results are consistent with studies of other organisms where the proportion of prey consumed decreases as prey density increases (e.g., Cook and Cockrell 1978; Sih 1980; Lucas

Table 5 Frequency with which salmon body parts were consumed by bears, as a function of fish species and sex, and site and year. Percent of females is the frequency of females when that part was eaten divided by the total number of females consumed that year. Hansen and Bear Creeks are located in the Bristol Bay area and the Chichagof (Chich) and Revillagigedo (Rev) Islands were located in southeastern Alaska. ND signifies not enough data for comparisons

Body Part	Site	Year	Species	Females (%)	Males (%)	χ^2	P
Body	Hansen	1997	Sockeye	32	44	64.1	<0.01
		1998	Sockeye	38	48	61.8	<0.01
	Bear	1997	Sockeye	39	40	0.0	0.89
		1998	Sockeye	57	57	0.0	0.98
	Chich	1996	Chum	7	26	28.0	<0.01
	Chich/Rev	1997	Chum	22	43	19.3	<0.01
			Pink	23	37	5.1	0.03
	Chich	1998	Chum	34	62	17.1	<0.01
			Pink	41	54	1.5	0.22
Belly	Hansen	1997	Sockeye	51	5	1074.0	<0.01
		1998	Sockeye	29	3	774.2	<0.01
	Bear	1997	Sockeye	36	1	34.0	<0.01
		1998	Sockeye	6	1	37.6	<0.01
	Chich	1996	Chum	85	44	74.5	<0.01
	Chich/Rev	1997	Chum	68	15	120.4	<0.01
			Pink	64	9	64.9	<0.01
		1998	Chum	68	56	3.0	0.09
			Pink	29	12	3.7	0.05
Hump	Hansen	1997	Sockeye	4	21	309.9	<0.01
		1998	Sockeye	2	16	357.3	<0.01
	Bear	1997	Sockeye	8	30	10.6	<0.01
		1998	Sockeye	5	16	50.4	<0.01
	Chich	1996	Chum	47	61	7.4	<0.01
	Chich/Rev	1997	Chum	4	11	8.7	<0.01
			Pink	4	24	18.8	<0.01
		1998	Chum	52	66	4.8	0.03
			Pink	30	32	0.0	0.89
Brain	Hansen	1997	Sockeye	10	25	168.5	<0.01
		1998	Sockeye	7	30	600.3	<0.01
	Bear	1997	Sockeye	16	34	5.5	0.02
		1998	Sockeye	20	43	85.9	<0.01
	Chich	1996	Chum	18	42	26.6	0.01
	Chich/Rev	1997	Chum	38	67	35.6	<0.01
			Pink	66	79	4.6	0.03
		1998	Chum	57	75	7.5	0.01
			Pink	54	78	6.1	0.01
Skin	Hansen	1997	Sockeye	0.3	0.4	0.8	0.38
		1998	Sockeye	0.2	0.1	0.9	0.35
	Bear	1997	Sockeye	ND			
		1998	Sockeye	ND			
	Chich	1996	Chum	ND			
	Chich/Rev	1997	Chum	8	2	7.8	0.01
			Pink	2	5	1.5	0.22
		1998	Chum	47	58	2.9	0.09
			Pink	14	12	0.1	0.76

1985) and anecdotal evidence from other bear-salmon studies. Shuman (1950) noted that bears rarely consumed most of the biomass of killed salmon when fish were plentiful and Gard (1971) reported that brown bears consumed most fish when salmon were scarce but would often kill, but not consume, many salmon when availability was high.

Partial consumption of salmon is possible in these systems for several reasons. First, our streams are small, clear, relatively shallow, and support healthy runs of spawning salmon, so bears require very little effort (both energy and time) to capture a fish. Flows are so low that stranding is often a major source of mortality in some sections of Hansen Creek (Quinn and Buck 2000) and the backs of male and even female salmon are exposed in much of the creek. A human can easily catch a salmon by hand in less than a minute and we have seen bears do so in a few seconds. Likewise, in SEA bears rarely need

Table 6 Percent of cases when a salmon body part was consumed by bears as it varies with spawning status of fish, 1994–1999

Body part	Chum				Pink				Sockeye	
	Females		Males		Females		Males		Females	
	Ripe	Spawned-out	Ripe	Spawned-out	Ripe	Spawned-out	Rip	Spawned-out	Ripe	Spawned-out
Body	23	20	41	11 **	46	8***	57	20**	22	35
Belly	92	9 ***	27	11	95	10 ***	19	1	95	56 ***
Hump	35	67 ***	44	52	45	46	41	40	5	9
Brain	41	37	43	44	62	51	85	53 **	18	5
Skin	24	2 ***	6	15	31	13 *	18	0	2	0
N	390	55	267	27	125	39	84	15	344	43

*$P<0.05$; **$P<0.01$; ***$P<0.001$

Table 7 Frequency with which body parts of sockeye salmon were consumed by bears, as a function of size class of salmon (body length; mid-eye to hypural plate). Data are % of fish in each size class when a body part was consumed. No consumption patterns were found when bears targeted the salmon skin or hump

Body part	Sex	Size class (mm)			
		350–400	401–450	451–500	501–550
Body	Female	12%	30	28	33
	Male	29	26	43	45
Brain	Female	3	5	8	15
	Male	15	18	23	29
Belly	Female	40	40	54	54
	Male	8	4	4	3

more than 60 s to secure a fish despite deeper flows and lower densities of spawning fish compared to our sites in Bristol Bay. The most common fishing behavior for bears in SEA is to stand in the stream and allow fleeing fish to swim toward them, at which point they pin a fish to the ground with their paws or jaws and carry it to the gravel bar to consume. Thus the energetic costs are often no greater than simply standing in the slow-flowing streams. Infrequently have we observed bears actively pursuing a fish (i.e., running upstream for several seconds).

Second, the energetic "reward" of salmon consumption varies with body parts and spawning status, resulting in dramatic differences in energy intake per unit feeding time for bears, depending upon which parts are consumed. When salmon enter freshwater, feeding is arrested, lipid catabolism increases, and biosynthesis of lipid in the liver decreases (Hatano et al. 1995), resulting in a fixed amount of energy, in the form of neutral storage lipids and protein, to fuel migration and reproduction (Gilhousen 1980; Brett 1995). For female salmon much of the lipid in the soma (all body parts except the gonads) is allocated to egg development (Hendry and Berg 1999). Consequently, roe is significantly higher in energy content (7.8 kJ/g wet weight) than somatic tissue (4.9 kJ/g wet weight; Hendry and Berg 1999). An average female sockeye salmon weighing 2 kg would contain about 400 g of roe (Hendry and Berg 1999). Thus a bear

targeting the roe would nearly double the energy intake over that from consuming only somatic tissue (assuming similar digestion and assimilation efficiencies for somatic and gonadal tissue; Pritchard and Robbins 1990). Multiplied over the course of the run, the energetic advantage for bears targeting high-energy body parts would be immense.

When interpreting our results, however, we used energy as the currency by which to assess consumption choice by bears. We feel justified in doing so because of the strong coupling between energy intake in the fall and reproductive success of bears. At the population level, density, average body size, and litter size increases with the availability of dietary meat, particularly salmon (Hilderbrand et al. 1999a). At the individual level, if bears do not achieve a certain body weight or level of fat accumulation prior to hibernation, reproduction will be inhibited (Rogers 1987; Stringham 1989a, 1989b; Samson and Huot 1995). Access to high-energy food is critical in the late fall as sufficient lipid reserves are needed to fuel metabolic costs during 4–6 months of hibernation (when no feeding occurs), as well as birth and lactation costs for females (Farley and Robbins 1995). Salmon are relatively high in energy, highly digestible (Bunnell and Hamilton 1983; Pritchard and Robbins 1990) and sufficiently aggregated that foraging efficiency may not necessarily limit intake rates, in contrast to other bear forage such as berries (Welch et al. 1997). It is unknown whether bears can achieve nutritional demands associated with successful reproduction without selective consumption (e.g., consuming ripe and spawned-out fish to the same degree or randomly consuming body parts). However, we assumed that bears that employ a foraging strategy that targets high-energy body parts or ripe fish will achieve better physiological condition and thus reproduce better.

Other factors may have influenced consumption choice besides energy intake. For example, the number of bears using the different habitats was unknown, thereby making it impossible to calculate the amount of salmon biomass available to each bear among habitats. Thus, two scenarios exist that might alter the interpretation of our results. If the ratio of bear biomass to salmon biomass was higher at the small ponds and

creeks, each bear would have a corresponding lower number of fish available to consume and thus would need to consume each fish to a greater degree. However, it is implau-sible that bears would congregate in higher densities in areas of lower food resources and thereby increase the potential for agonistic interactions. Alternately, if the bear:salmon biomass ratio was higher at the large ponds and Hansen Creek, we would expect more biomass to be consumed per fish at these sites, inconsistent with our results and counter to foraging theory predictions (Stephens and Krebs 1986). Further studies of the costs associated with acquisition and consumption of salmon, time spent on streams, and sex- and spawning status-specific energetic rewards will help interpret our results.

Salmon attributes

At all sites and during all years, ripe fish were consumed by bears to a greater degree than spawned-out fish. Bears probably consumed less biomass per spawned-out female because the favored body part (roe), which constitutes 15–20% of the body weight (Brett 1995), was no longer present. We often observed bears catching and releasing salmon and, although our sample size was small (*n*=12), bears only released spawned-out females and retained all ripe females. Of those spawned-out fish that were retained, bears often sniffed at the anus, presumably to check for the presence of eggs and, upon discovering females were spawned-out, often consumed only the brain or abandoned the carcass altogether. Similar behavior was observed for black bears foraging on pink and chum salmon at Olsen Creek, Alaska (Frame 1974) and brown bears foraging on sockeye salmon in the Karluk River system, Alaska (Shuman 1950). Likewise, Quinn and Buck (2000) found that ripe females were more often scavenged than spawned-out females at Hansen Creek, Alaska.

Spawned-out males were also consumed to a lesser degree than ripe ones, suggesting that differences in consumption according to spawning status were not simply a function of whether desired body parts were present or absent (as might be the case for females with eggs). For example, the body flesh was consumed more often in ripe versus spawned out males. The body flesh of ripe males is relatively high in neutral storage lipids upon entrance into fresh water, but the lipids are gradually used up developing secondary sexual characteristics and fueling movements while in the stream (Ando et al. 1985; Hendry and Berg 1999). As in-stream life lengthens, males spawn out and the somatic tissue becomes nearly devoid of energy (both lipid and protein) (Gilhousen 1980; Hatano et al. 1983; Brett 1995; Hendry and Berg 1999). With a loss of energy there is a concomitant loss in skin pigmentation as white streaks develop along the dorsal ridge and the skin loses its smooth sheen, becoming covered with scars, fungus and dry areas. It is easy for humans to estimate the length of time a salmon has been in the stream and it would not be surprising if a bear could do likewise.

Consumption of other body parts did not appear to be influenced by spawning status but this was also probably a function of the type of lipid present. For example, the frequency of brain consumption occurred irrespective of spawning status, similar to results found for black bears feeding on salmon at Olsen Creek, Alaska (Frame 1974, but see Reimchen 2000). Although the body fat is largely used up by salmon during migration and spawning (Gilhousen 1980; Hatano et al. 1983; Brett 1995; Hendry and Berg 1999), the fat associated with the nervous system and brain is presumably less affected. The brain is high in structural phospholipid (e.g., Buda et al. 1994), which is not transferable for gonad development as is the case for neutral fat stores (primarily triacylglycerols; Jobling 1994) in the somatic tissue (Ando et al. 1985; Hendry and Berg 1999). Thus, energy content in the cranial region may not decline precipitously as in-stream life increases and bears would achieve similar energetic rewards by feeding on the brain region irrespective of spawning status. Furthermore, the lipids in brains of cold-adapted fish (and presumably salmon) are relatively high in ω–3 and ω–6 long-chain polyunsaturated fatty acids (e.g., Buda et al. 1994) which have low melting points and thus maintain fluidity (function) during periods of prolonged cold stress. Organisms that experience large fluctuations in thermal stress, such as those that undergo long hibernations (bears), must either synthesize these fatty acids or obtain them from their diet (e.g., Farkas et al. 1980; Frank 1994; Fodor et al. 1995). Thus, by targeting the salmon brains, bears may intake these essential fatty acids which help control membrane physical state during hibernation.

Bears generally consumed a similar biomass per fish for both males and females within species but showed remarkable differences in the body parts eaten. The belly region was targeted in females, presumably reflecting a preference for roe over testes due to the high lipid content in roe (see also Mossman 1958; Gard 1971; Frame 1974). Interestingly, the male salmon that had their bellies consumed were smaller than those not bitten in this region, suggesting that bears may sometimes mistake small males for females. The dorsal ("hump") area was more often bitten in males than females. The hump is a secondary sexual characteristic, most likely evolved for male display in intra-specific competition or female choice, and is much larger in males than females (Quinn and Foote 1994). There is no indication that male humps contain elevated levels of energy or nutrients; it may simply be the area where bears first bite in the process of securing the fish (see also Frame 1974). We have often seen bears carrying fish into the forest by the hump, and have seen males alive in the streams with open wounds in the dorsal region, suggesting that they escaped from the jaws of the bear.

We also documented a higher frequency of consumption of the brain region in males than females. It is unlikely that the amount of lipid stored in the cranial region

of males is greater per body weight than females but the absolute amount probably increases with body size and males are generally larger than females (Groot and Margolis 1991). The brain region was also eaten more often in larger individuals for both sexes of sockeye salmon, similar to results found for black bears feeding on chum salmon in British Columbia (Reimchen 2000). This suggests that the energetic reward in targeting the brain region may be a function of fish size rather than sex. The brain region is high in lipids (Gende and Quinn, unpublished data) but bears must also consume cartilage that may lower the digestibility of this body part. We have often observed bears lapping at the brain region after consuming it, suggesting that the bears seek the brain rather than the cartilage.

Understanding factors that affect variation in consumption has important ecological ramifications. Bears act as "engineers" of nutrient transfer in riparian areas when they feed on salmon because they defecate (and urinate) digested fish material and drag carcasses into the forest, thereby transferring marine-derived nutrients front the aquatic to the terrestrial systems (Bilby et al. 1996; Ben-David et al. 1998; Willson et al. 1998; Hilderbrand et al. 1999b). The marine-derived nutrients and energy in salmon tissue enhances freshwater productivity (Wipfli et al. 1999) and is also utilized by riparian plants and animals (Bilby et al. 1996; Ben-David et al. 1998). Thus, partial consumption of salmon affects the energy and nutrients available to both the aquatic and terrestrial foodwebs (Mathisen et al. 1988; Cederholm et al. 1989; Willson and Halupka 1995; Bilby et al. 1996, 1998; Willson et al. 1998; Wipfli et al. 1998). We present data that are a first step in quantifying the relationship between salmon density and salmon consumption, yet more data are needed on the time required to catch and process salmon, the energetic content of the fish, and the densities of bears using salmon streams. Such data will provide critical information regarding the ecological interactions between bears and salmon, minimum numbers of salmon needed to sustain bear populations, and the movement of nutrients between aquatic and terrestrial habitats that depends on these interactions.

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